

## NOTES AND NEWS

NOTES ON CONES AND VERTEBRATE-MEDIATED SEED DISPERSAL OF *Pinus albicaulis* (PINACEAE).—The literature is unclear as to the events following ripening of *Pinus albicaulis* cones. Sudworth (For. trees Pacific slope. 1908) wrote that cones mature in late August or early September and release their seeds in September or October. "The cones dry out and open slowly . . ." This information is contradicted by Shaw's classification (The genus *Pinus*. 1914) of *P. albicaulis* in *Cembrae*, a group characterized by indehiscent cones. Subsequent authors acknowledged the indehiscence of *P. albicaulis* cones but were confused about dispersal mechanisms (e.g., Bowers, Cone-bearing trees Pac. Coast. 1956; Peattie, Nat. hist. w. trees. 1953). Krugman and Jenkinson, who had access to experimental data, suggested that "seeds are dispersed when the detached cone disintegrates" (In: Schopmeyer, ed., Seeds woody pls. U.S. 1974). However, information on cone disintegration and subsequent seed dispersal comes mainly from experiments in which cones were protected and does not elucidate the true fate of cones and seeds.

I have gathered cone-fate information from 1973 to 1979 in various locations in Inyo, Mono, Mariposa, and Tuolumne Counties in the eastern Sierra Nevada, California. When *P. albicaulis* cones ripen, the scales separate slightly from the core of the cone (thus, the cones are not completely indehiscent); yet, the scales hold the seeds firmly in place and are not easily dislodged. Cones I collected in 1975 still retain their seeds.

The large, wingless seeds are an attractive food for many birds and rodents. Clark's Nutcracker (*Nucifraga columbiana*) is sympatric with *P. albicaulis* wherever the pine occurs. From midsummer until the cones ripen, nutcrackers forage preferentially on unripe seeds of *P. albicaulis*. Nutcrackers harvest seeds by jabbing their bills repeatedly into the top or sides of cones to loosen and tear off scales. Only rarely do they first detach a cone from a tree before removing seeds. Ripe seeds are taken in quantity and stored in small "caches" consisting of 1 to 15 seeds each (median = 4) in selected "storage slopes" and throughout the forest terrain. I calculated that each nutcracker may store as many as 32,000 *P. albicaulis* seeds each year at subalpine elevations. These seed caches are retrieved by nutcrackers in spring and early summer (Tomback, Ph.D. diss., Univ. California, Santa Barbara. 1977a; Tomback, Living Bird 16:123-161. 1977b; Tomback, Condor 82:10-19. 1980). However, many of the seeds are placed in microhabitats favorable to germination and seedling survival. By mid-October, some seeds have been removed from many *P. albicaulis* cones by Clark's Nutcrackers. These cones are partly or completely hollowed out with little of the cone intact and a shell of closed scales on the underside of the cone (Tomback, 1977a, 1977b, op. cit.).

My studies of Clark's Nutcracker suggest that this bird is an important disperser of *P. albicaulis* seeds. Several kinds of circumstantial evidence, such as seedlings originating in nutcracker seed caches, seedling clusters from caches producing a "multi-trunked" growth form (Clausen, Evolution 19:56-68. 1965; Lueck, M.A. thesis, Oregon State Univ. 1980), the sites selected by nutcrackers for seed caches, and a consideration of alternative dispersal mechanisms, support the hypothesis that the interaction between the nutcracker and *P. albicaulis* is mutualistic and coevolved. A similar interaction was proposed for the nutcracker and *P. edulis* (Vander Wall and Balda, Ecol. Monogr. 47:89-111. 1977). More direct evidence is required to substantiate both of the proposed interactions.

During late summer and early fall, Douglas squirrels (*Tamiasciurus douglasi*) cut down numbers of *P. albicaulis* cones and bury them in middens. Chipmunks (*Eutamias* spp.) climb into trees and gnaw on the cones to extract seeds. A chipmunk-foraged cone has a distinct appearance: all but the proximal and distal scales are gone, leaving only the core. Chipmunks as well as deer mice (*Peromyscus maniculatus*) are known to cache germinable pine seeds (West, Ecology 49:1009-1011. 1968; Abbott and Quink, Ecology 51:271-278. 1970).

Other mammals and birds take *P. albicaulis* seeds when cones are ripe (Tomback, 1977a, 1977b, op. cit.): e.g., golden-mantled ground squirrel (*Spermophilus lateralis*),

Williamson's Sapsucker (*Sphyrapicus villosus*), White-headed Woodpecker (*Picoides albolarvatus*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), Cassin's Finch (*Carpodacus cassinii*), Red Crossbill (*Loxia curvirostra*), and Pine Grosbeak (*Pinicola enucleator*). With such diverse foraging on *P. albicaulis* cones by vertebrates it is likely that few seed-bearing cones, if any, remain on trees by late fall. Vertebrate foraging has also been observed to "destroy" an entire seed crop of *Pinus lambertiana* (Tevis, J. Wildlife Managem. 17:128-131. 1953) and *P. flexilis* (Clements, Pl. succession. 1916).

To test the hypothesis that most *P. albicaulis* seed dissemination is effected by vertebrates, particularly Clark's Nutcracker, it is necessary to gather information on the condition of old and new cones encountered in the field. Here, I present the results of a preliminary study.

On 9 and 10 August 1979, I surveyed *P. albicaulis* on the east and west slopes of Cathedral Peak, Yosemite National Park, Tuolumne and Mariposa Counties, California. On the east slope I observed the occurrence of old cones in a pure stand between 3050 m and 3250 m (25° slope). For each of the 36 trees along a line transect, I noted the number of old cones visible from my position and tree growth form (following Clausen, 1965, op. cit.). The number of old cones per tree ranged from 0 to 30 [ $\bar{x} = 4.9 \pm 1.5$  s.e.]. Proportions of trees encountered in each growth form category are as follows: *erect trunk*: 0.44; *elfinwood*: 0.44; and *intermediate*: 0.11. Fifty percent of the trees had no old cones. One old cone had been nutcracker-foraged, and the remainder were cores, such as those left by chipmunks. A linear regression analysis of number of old cones per tree vs. elevation indicated a significant negative correlation ( $r = -0.641$ ,  $p < 0.001$ ), which is probably the consequence of lower cone productivity of the krummholz or "elfinwood" growth form (Tranquillini, *Physiol. ecol. alpine timberline*. 1979). A One-sample Runs test (Siegel, *Nonparametric statistics*. 1956) confirmed a significantly greater occurrence of the elfinwood growth form as elevation increased ( $p = 0.025$ , one-tailed). On 8 September 1979, I surveyed the east slope of Cathedral Peak for new cones, repeating the same transect. Only 7 trees bore new cones (none of the elfinwood), and all new cones were partly or completely harvested by nutcrackers and chipmunks.

The transect on the steeper (30°) west slope of Cathedral Peak zigzagged over a strip ca. 50 m wide from about 3050 m to 3200 m. Predominantly erect *P. albicaulis* are scattered over the lower regions of the slope, whereas dense elfinwood mats occur in talus above ca. 3200 m. At the very top of the slope where there is some shelter, trees intermediate in growth form occur. For the 44 trees on the transect, I noted the following frequencies of cone occurrence: *no cones*: 0.43; *old cones*: 0.45; *new cones*: 0.39; *old and new cones*: 0.27; *vertebrate-foraged new cones*: 0.23. Thus, by 10 August, vertebrates had opened 59 percent of the new cones. All the old cones observed were either cores or hollow shells.

During September, 1979, I surveyed *P. albicaulis* in other areas to assess the condition of new cones. On 10 September, trees were examined in the vicinity of Budd Lake, Yosemite National Park, Tuolumne Co., California, 3050 m (Table 1). Nutcrackers had foraged in 75 percent of the new cones observed. Fifteen trees on each of three different slope aspects were surveyed on 15 September on the west slope of Mammoth Mountain, Mono Co., California (Table 1). Altogether, 78 percent of the new cones were completely or partly destroyed by nutcrackers and chipmunks. (From the data reported, it is apparent that the 1979 *P. albicaulis* cone crop was only fair to moderate in the central Sierra Nevada.)

During 6 to 10 August and 1 to 3 September 1979, I examined 28 old cones found on the forest floor in both the Cathedral Peak and Kearsarge trail-Kearsarge Lakes areas, Mono and Fresno Counties, California. The cones were categorized as follows: *chipmunk cones*—11%, *disintegrating cones* (loose scales)—21% *nutcracker-harvested cones*—21%, *small, closed cones* (ca. 5 cm diameter)—46%. Intact old cones on the ground were rare in all study areas. I pried open the closed cone scales of the small cones encountered and found only white-coated empty seeds. Thus, vertebrate-foraged cones

TABLE 1. MEAN NUMBER PER TREE AND STANDARD ERROR OF NEW AND VERTEBRATE-FORAGED CONES.

Date	Location	Total trees surveyed	New cones per tree	Vertebrate-foraged cones per tree
10 Sep 1979	Budd Lake	10	2.1 ± 0.46	1.6 ± 0.54
15 Sep 1979	Mammoth Mt.	45	2.0 ± 0.47	1.6 ± 0.41

accounted for 32 percent of the cones sampled, and sterile cones accounted for 46 percent.

These data suggest that few if any seeds of *P. albicaulis* remain after vertebrates cease foraging in late fall. It is possible that any remaining cones with a full or partial complement of viable seeds disintegrate and/or abscise soon after this time. Abscission may, in part, be a weight-dependent process, which would explain why only the lighter, vertebrate-harvested old cones remain on the trees. Also, some cones seem more resistant to disintegration, such as those hollowed out by nutcrackers and small, sterile cones.

If so few cones escape vertebrates each year, is cone disintegration the primary seed dispersal mechanism for *P. albicaulis*? Seed-storing vertebrates, particularly Clark's Nutcracker, appear mainly responsible for *P. albicaulis* population recruitment. Not only do nutcrackers and some rodents place a large percent of seeds in sites favorable to germination and seedling survival, nutcrackers transport seeds to storage sites some distance from parent trees (Tomback, 1977a, 1977b, op. cit.). Consequently, nutcracker seed dispersal helps maintain the "pioneering" status of *P. albicaulis*. Seeds released by cone disintegration have lower reproductive value than those stored by nutcrackers and rodents. Because the seeds are large and wingless, many will drop near the parent tree. Thus concentrated, they may be consumed in quantity by seed predators and, because *P. albicaulis* is shade intolerant (Baker, Principles silviculture. 1950), they are less likely to end up in conditions favoring seedling survival. In addition, "pioneering" may be an important reproductive tactic of the species.

Why are *P. albicaulis* cones, as well as cones of other species in Subsection *Cembrae* (classification of Little and Critchfield, Subdiv. genus *Pinus*, U.S.D.A. Misc. Publ. 1144. 1969) indehiscent? All *Cembrae* species are sympatric with one or more subspecies of the Eurasian Nutcracker (*N. caryocatactes*) (Dement'ev, Birds Soviet Union. 5. 1970) or with Clark's Nutcracker. In a nutcracker or rodent dispersal system, natural selection should optimize the number of seeds available to dispersal agents. "Packaged" seeds should attract birds and rodents, increase their foraging efficiency, and thereby maximize the number of seeds stored in favorable sites. Consequently, indehiscent cones should maximize the reproductive success of any pine with vertebrate-dispersed rather than wind-dispersed seeds.

It is interesting to note that the seeds of *Pinus sabiniana* and *P. torreyana* (Subsection *Sabinianae*, Little and Critchfield, 1969, op. cit.) are large and bear non-functional wings, although the cones are dehiscent. The seeds are released over a period of several months (Krugman and Jenkinson, 1974, op. cit.). These pines may be evolving vertebrate seed dispersal. Either they do not have the genetic potential for indehiscent cones, or the seeds may be dispersed by a facultative tactic: seed-storing vertebrates—such as *Peromyscus* (McCabe and Blanchard, Three species *Peromyscus*. 1950) and Scrub Jays (*Aphelocoma coerulescens*), which cannot take seeds from the massive, closed cones—and seed fall. This also applies to *P. flexilis* (Subsection *Strobi*, Little and Critchfield, 1969, op. cit.), which has dehiscent cones. Nutcrackers and rodents, as well as seed fall, may disperse the large, wingless seeds of this species (Vander Wall and Balda, 1977, op. cit.; Tomback, Condor 82, in press. 1980).

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AGGREGATION OF *Prunus ilicifolia* (ROSACEAE) DURING DISPERSAL AND ITS EFFECT ON SURVIVAL AND GROWTH.—Dispersing seeds are commonly aggregated at settlement, by vertebrates voiding cohorts of ingested seeds or storing seeds in caches, or by ants collecting and discarding seeds with elaiosomes. Aggregation may have significant consequences for seed and seedling survival and growth. For buried seed, aggregation may increase successful emergence (Linhart, J. Ecol. 64:375–380. 1976.). Seed predation may increase with cohort size (Wilson and Janzen, Ecology 53:954–959. 1972.) or decrease as aggregation lowers seed density over most of the dispersal region. Likewise, later herbivory might be increased or decreased. However, competition among aggregated seedlings surely must be greater than among widely scattered plants. None of these effects has been widely studied, perhaps for technical reasons or for lack of data on post-dispersal seed distributions.

In the California chaparral, seeds of *Prunus ilicifolia* are commonly dispersed by *Canis latrans*, with defecated and vomited cohorts containing 4–66 seeds (mean  $23.5 \pm 2.4$  s.e.,  $n = 34$ ) in the central Santa Monica Mountains (1975, 1977, 1978), and 3–6 seeds at Chalone Peak, San Benito County ( $n = 4$ , 1974). This compares with seed cohorts of *Washingtonia filifera* dispersed by *Canis latrans* in eastern San Diego County, of 1–275 seeds ( $48.7 \pm 3.1$ ,  $n = 252$ ; Bullock, Principles 24:29–32. 1980.). The endocarp/seed units of *Prunus* weighed  $1.46 \pm .04$  g ( $n = 143$ ), and *Washingtonia* seeds weighed 0.10 g ( $n = 50$ ).

Experiments were conducted to observe survival and growth of *Prunus ilicifolia*, particularly with reference to aggregation of the seeds. Seeds were collected in the Santa Monica Mountains, and grown at the University of California, Los Angeles, in silty loam 25 cm deep resting on the natural substrate. The plants had only partial morning shade, and were watered only by rain. From December 1973 to November 1974, plants were grown in  $1 \times 2$ -m plots with 50 seeds each in four unreplicated conditions of inter-seed spacing: 20 cm, 10 cm, 5 cm, and 0 cm. Also in this year, cohorts (0 cm seed

TABLE 1. SURVIVAL FROM SEED TO FIRST-YEAR SEEDLING AND MEAN ABOVE-GROUND DRY WEIGHT OF SURVIVORS ( $\pm$  s.e).

Aggregation	n	Survival	Biomass (g)
Seed spacing (cm)			
0	50 seeds	0.74	$2.9 \pm 0.5$
5	50	0.64	$6.1 \pm 1.2$
10	50	0.20	$6.2 \pm 1.5$
20	50	0.22	$1.4 \pm 0.3$
Seeds per cohort			
4	7 cohorts	0.79	$14.9 \pm 2.9$
2	7	0.50	$12.1 \pm 2.3$